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COLLECTED PAPERS

of

C. Herbert Hurst

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1

THE STRUCTURE AND HABITS OF ARCHÆOPTERYX.

By C. H. Hurst, Ph.D.

Plates XIV., XV., XVI.

I.—The Skeleton of Archæopteryx.

Apart from a single feather, only two specimens of *Archæopteryx* are known, and it is possible that these may not be identical in species or even in genus. So far as we know them, the differences between the two appear, to those who are best qualified to judge, to be too small to justify separation into two species. Though both were found in Bavaria, I shall refer to them as the "Berlin specimen" and the "London specimen" respectively.

It is not convenient to begin with a description of the external form of the bird, as is customary with recent species, for that external form can only be guessed at with reasonable chance of guessing accurately after a careful consideration of the structure of such parts as are still preserved. This is even more conspicuously true of the habits of the animal.

Of the skeleton, if we assume the two specimens to be so nearly related that the characters exhibited in either may be taken as true of both, we have quite an extensive knowledge.

The *vertebral column* is readily divisible into four regions: cervical, trunk, sacral, and caudal. Whether the vertebræ are fully ossified or not it is difficult to say. I can find no justification for the statement that they are amphicoelous. Professor Dames tells me that his statement to that effect is a mere slip of the pen, and that he intended only to say that, so far as can be seen in a specimen in which the vertebræ are still in their natural relations with one another, the ends are flat and not as in most birds, saddle-shaped. The central or internal part of each vertebra in the London specimen is stated by Owen to be represented by a deposit of crystalline "sparry matter" in the caudal region, while the outer "crust" has adhered to the upper slab or

"counterpart." Whether this really shows that the vertebræ (of the tail) were mainly cartilage or other soft tissue with only a crust of bone or not, may be open to question. The perfectly-fitting joints, the large transverse processes of the anterior caudal vertebra, and the slenderness and stiffness—as shown by the straightness of the tail in both specimens—of this region of the vertebral column are strong evidence that the bones were *well-ossified.*

Of the nine *cervical vertebræ*, only eight are well-preserved, the first being almost unrecognisable. Measuring the lengths of the centra of these on a large photograph (scale $\frac{132}{137}$), I make the sum of the eight in the Berlin specimen to be about 75 mm.; but Professor Dames gives numbers which together make only 60·5. A glance at Plate XV. will show the position of the neck in this specimen. It is very strongly arched so as to bring the head almost into contact with the back of the animal in the region of the thorax. It is difficult to make these measurements accurately in either the specimen or the photograph, but the discrepancy between the two measurements is too great to be accounted for by this difficulty, and I suspect that Professor Dames' measurements have been made along the inner curve—*i.e.*, through the neural spines—while mine were made near the ventral curve, *i.e.*, through the centra of the vertebræ. I suspect, therefore, that when the animal's neck was straightened out it would be 75 mm. long in addition to the length of the atlas, which may be taken to be a very small quantity as in modern birds. Of the nine cervical vertebræ the middle ones are longer than those nearer the ends of the neck, the fifth being the longest.

Cervical ribs, apparently movably articulated, may be made out, and there appear to be eight pairs of them. The neural arches and spines are well-developed and strong, the spines being 2 to 3 mm. high.

The *trunk vertebræ* being somewhat displaced, and the vertebral column distorted, it is not very easy to make sure of their number. There appear, however, to be ten, measuring together about 70 mm. The vertebræ appear to be almost equal in size, and nine of them bear *ribs*. There are also *ventral ribs*, resembling the "*abdominal*" *ribs* of the geckos and chamæleons, and clearly showing the ventral boundary of the abdominal cavity (*see* 14 in Plate XV.).

The *sacrum* is hidden in the Berlin specimen except at its ends.

It measures 26 mm. in length. It is probable that there are about seven sacral vertebræ.

The *vertebræ of the tail*, twenty in number, measure together about 170 mm.—slightly less perhaps. The first few are very short and stout, each measuring about 4 mm. in length and 4 mm. in height. The first four have well developed transverse processes; in the fifth this process is not well preserved, and the vertebræ behind this have no transverse processes, but only a ridge. The vertebræ are longest nearer the middle of the tail, the eleventh measuring nearly 12 mm. The tail as a whole seems to have had little flexibility, for it is almost perfectly straight in both specimens. The tale of the London specimen has apparently only eighteen vertebræ and measures 180 mm.

The *skull* has been much further exposed since the photograph was taken. It is large and fairly massive, the jaws are stout, and teeth are very easily made out in the upper jaw. Those of the lower jaw are, however, hidden by those of the upper, and it is impossible to say at present how many there were. The sclerotics are ossified. The hinder part of the skull is destroyed in the Berlin specimen, and it is worthy of note that the cranial cavity was not filled with matrix. No part of the skull is recognisable with certainty in the London specimen, though it may be that the supposed cast of the brain (!) is a portion of the skull.

The *ribs*, both vertebral and ventral, are very slender. There are no uncinate processes visible.

Of the *sternum* nothing is known, though much has been written. In the Berlin specimen it probably lies still hidden in the matrix. The position of the ventral ribs shows that it must have been small.

The *scapulæ* in the Berlin specimen were broken in exposing the specimen. The right one is easily recognisable in Plate XV. They are flat curved bones, not unlike those of a modern bird. Their length is 43 mm. or thereabouts, according to Dames. In the photograph only a portion is seen.

The *coracoids* are in the Berlin specimen largely hidden. I have not specially examined what portion is exposed in the London specimen. The dorsal ends are exposed in the Berlin specimen and possess a furcular tuberosity as in other birds.

Of the *furcula*, a small portion is seen at the left shoulder of the Berlin specimen. It was, however, imperfectly exposed at the time when the photograph was taken. A larger portion is seen in the London specimen. It is a characteristically avian furcula, U-shaped ventrally, and articulating with the furcular tuberosity of the coracoid at each shoulder.

The *humerus* is a well-developed bone in each wing. Its form and dimensions may be seen in Plates XIV. and XV. It differs from that of other birds in being devoid of the pectoral crest or ridge for the insertion of the great pectoral muscle. As Dames points out, this confirms his view that the sternum must have been small, as must also the great pectoral muscle. In Plate XIV. the proximal end of the humerus is covered by a portion of the matrix, which has since been removed (at 11 in Plate), and that plate consequently gives an impression of a humerus which is slightly shorter than the true length.

The bones of the fore-arm, seen in Plates XIV and XV, are a straight *radius* 55 mm. long, and a *curved ulna* 56 mm. long.

The *carpus* offers great difficulties. Owen figures two bones, one of which is visible in the London specimen. Why he should ignore the enormous ulnar carpal, which is a conspicuous object in the London specimen, need not here be discussed. It is conspicuously shown in Fig. 2 and in Plate I of Owen's memoir, where it is numbered 56′ and described (presumably with the radial carpal) as "left carpus" (it being probably a part of the right carpus), and something wholly unlike it is put in its place, in dotted lines, in his second plate (Fig. 2).

Of these bones I have seen two clearly, one being the radiale (4 in Plate XIV), which is visible in both the specimens, the other the "ulnare," visible only in the London specimen. In the Berlin specimen the carpus lies radial side uppermost, and it is not surprising that, like some other parts, the ulnar portion of the carpus lies still embedded in the matrix. This is even admitted by Dames. The little bone called "ulnare," and drawn from imagination by Owen, and also drawn by Dames, may or may not be present. I have tried, and failed, to make it out in the Berlin specimen, and I have also tried, and failed, to make sure that it is not there. One thing only I can say of it, viz., if present it is probably the *intermedium*, and not the ulnare. The "ulnare" is the enormous and conspicuous bone shown

at the distal end of the right radius and ulna. It is for a carpal bone, of enormous size, and I am not prepared to believe that it played no part in the support of the metacarpals.

Of the distal row of carpals it is only possible to say that they are not recognised in either specimen. Whether they have fused with the metacarpals, as they do in modern birds, or were cartilaginous and so not preserved, or were fused with the bones I have referred to as belonging to the proximal row; or whether the two figured by Owen and Dames are the proximal row, and the large bone I have called "ulnare" is really, as the London specimen suggests, a fused mass representing the whole or part of the distal row of carpals, can only be decided, so far as I can see, by one of two consummations "devoutly to be wished"—(1) the excavation of the exceedingly thin and fragile Berlin slab *from the back*, or (2) the discovery of fresh specimens. The first of these involves too great a risk to what it is hardly an exaggeration to say is the most valuable palæontological specimen in any museum in the world.

To admit that one does not know what that bone is, is one thing; to ignore its existence is another. Whether it be right or wrong, I shall for the present call it the *ulnare*. Subsequent proof that it is something else, *e.g.*, a crocodilian "lenticulare," or, as seems not improbable, *unciforme*, will not invalidate my argument.

The *hand* has been much misrepresented both in words and in drawings. There are *five digits* and no fewer, and I never suspected that it would be necessary for me to give further proof than that already given in my essay on errors. This conclusion, however, having been controverted, I will venture now to prove it over again by three distinct proofs, each of which is in itself conclusive.

(1.) Three *long, slender* fingers on each hand are plainly seen on the Berlin slab. They are made up of two, three, and four phalanges respectively, in addition to a metacarpal each. Each bears a claw, which, though not easily made out in the photographs, especially in the smaller photographs, is perfectly distinct in most cases in the slab itself. There can be no doubt, and nobody does doubt, that these three correspond to the digits I, II, and III respectively of the normal pentadactyle reptilian fore-limb. The lengths of the various metacarpals and phalanges in the Berlin specimen are as follows, beginning at the proximal end, *i.e.*, with the metacarpal, in each case:—

I. $8 + 20 + 11 = 39$ mm.

II. $27{\cdot}5 + 15 + 19 + 13 = 74{\cdot}5$ mm.

III. $26 + 5{\cdot}5 + 4 + ? + ? = 44{\cdot}5$ mm. The joint between the third and the ungual phalanx is hidden, but these two together measure 19 mm. Of these bones the second metacarpal is the largest, and at its basal end it is under 4 mm. thick.

Some of the bones corresponding to these are to be seen in the London specimen: but as they are displaced, it is not possible to identify them with certainty. What Owen called the two terminal phalanges of the digit I, closely resemble the two terminal phalanges of digit II of the Berlin specimen, and I take them for these phalanges. They measure respectively 22 mm. and 15 mm., *i.e.*, they exceed the bones of the Berlin specimen in the proportion of rather over 9 to 8. To justify this determination I give the lengths of some other bones in the specimens. The first number in each case is the length of the bone in the Berlin specimen; the second, that in the London specimen. Ulna, 56 mm., 63·5 mm.; Radius, 55 mm., 62 mm.; Femur, 51 mm., 58 mm. (?); Tibia, 71 mm., 81 mm. In each case except that of the femur the ratio is almost exactly 8 : 9, and in the case of the femur it is impossible to measure the exact length in the Berlin specimen. The numbers of vertebræ in the tails differ in the two specimens, so that it will not be safe to take the ratio in length of the two tails as a guide. There is no other bone which can be identified and measured with certainty in both specimens, so we may adopt 8 : 9 as the relative sizes of the Berlin and the London specimens respectively.

But in thickness a different relation holds. In corresponding bones of two similar animals we find that the ratio of thickness to length is always greater in the larger animal. And this is true here: all bones of the London specimen are stouter and more massive than those of the Berlin specimen. Now, in the London specimen two conspicuous bones were identified by Owen as the "third" and "fourth" metacarpals. They measure 39 and 33·5 mm. respectively in length. In thickness they are much greater than any hand-bone of the Berlin specimen. Others have regarded these bones as the second and third metacarpals. Suppose this were the case, then we get these ratios between the London and Berlin specimens.

39 : 27·5 = more than 11 : 8 and 33·5 26 which is 10·3 : 8. Further, the bones are utterly unlike their supposed equivalents in the Berlin slab. They are far stouter, and the longer of the two is exceedingly broad at the base, and therein is well-fitted to resist torsional stress or twist at the joint. In their proximal halves, instead of being slender and almost circular in section, they are stout and have ridges which, when the two were fitted together, would have prevented their movement one on the other. Whatever they are, they are utterly unlike any bones visible in the Berlin specimen. Their position with reference to the feathers of the wing, in spite of the dislocation of other bones, is just that of the large metacarpals in an ordinary bird's wing; and the fact that these feathers are still in their normal position in this wing (the left) justifies the belief that when the animal finally settled down previous to fossilisation those feathers were still bound to those metacarpals by ligament.

This is proof no. 1 that those two bones are the metacarpals of the digits IV and V.

(2.) The second proof is a more formidable one. Some hundreds of experiments extending over hundreds and even thousands of years have shown the effect of "selection" upon dogs, horses, sheep, pigs, pigeons, poultry, vines, roses, plums, apples, pears, strawberries, gooseberries, blackberries, pansies, daisies, dahlias, chrysanthemums, etc., etc., and the result is the same in all cases. Selection occurs in Nature (Naudin, Darwin, Wallace), and its effect is the same as in the case of artificial selection (Naudin, Darwin, Wallace, Bates, and others). I do not think it necessary to repeat the proof of this statement here: the proof is far too long, too well known, and too widely accepted for me to need to say more about it.

We may, therefore, take it as proved that the form and dimensions and structure of every bone and feather in *Archæopteryx* is the outcome of long-continued Natural Selection. The form and structure of the bones of the three digits visible in the Berlin specimen, and of the feathers in the same specimen, show what the conditions of selection have been, and what have been the uses of those several parts.

The digits I, II, and III are long, *slender*, and clawed. Each metacarpal and phalanx is concave on the flexor surface. The ends of the bones are curved like pulleys, allowing of free movement at every

joint. A distinct tubercle, for the insertion of the flexor tendon, is recognisable at the proximal end of almost every one of the eighteen phalanges, and these, together with the curvature of the bones, show that flexor muscles were well developed and active and useful, and, in view of the forms of the joints, were useful in producing extensive flexion of those digits. One of these joints has been referred to by some who had not seen the specimen as possibly a fracture (the joint between the second and first phalanges of the third digit, marked 16 in Plate XV); but a more perfect joint does not exist in the toe of any existing bird than that joint. It is perfectly preserved, and nobody who has seen it can doubt for a moment that it has been evolved under the influence of Natural Selection, and was exceeding well-adapted to allow of a very extensive flexion.

The feathers are as perfectly adapted to resisting the passage of air through them as in any modern bird. Those who have studied the mechanism of flight in detail will recognise why those feathers are all so curved that the dorsal surface of the wing when at rest is *convex*; why the anterior division of each vane is narrower than the posterior one, and is strongly curved and overlaps the posterior division of the vane of the next feather in front. They will know that such a wing is useful only if adequately supported by rigid bones capable of resisting very considerable torsional stress.

These two sets of structures—the digits I, II, and III, and the feathers—have been evolved under the direction of Natural Selection. They are both, therefore, fitted to perform the functions they actually did perform. The digits were useful for some purpose involving extensive flexion: they were, in fact, used to grasp parts of trees—for I shall show later that the animal did not habitually walk on the ground on all fours. They could not do this if those large feathers were attached to them. Mr. Pycraft has shown that in *Opisthocomus* the young use the digits for climbing, and that in order to enable them to do so the development of the mid-digital and ad-digital quills is delayed till such time as the young are able to fly or to climb without the help of these digits. I thank him for this excellent illustration (NAT. SCI., vol. v., pp. 355 and 358). It confirms the opinion I have expressed that flexible digits cannot be used for climbing if they bear large quills.

And again, the digits I, II, III of *Archæopteryx* (which the large size and perfectly ossified bones show to be an adult, as also do the well-developed feathers) are, by virtue of their very great slenderness and narrowness at the joints, incapable of resisting a great torsional stress. Unless those feathers exert a great torsional stress on the bones supporting them they are useless. I have shown they were not useless. Therefore they exerted a great torsional stress, and therefore they were supported by bones not yet seen in the Berlin specimen, although those of the left wing are seen in the London specimen. It follows, therefore, that the first three digits were used for climbing, and that one or more others were present to support the feathers.

(3.) The third proof is incomplete. It shows only that the digits I, II, and III did not support the feathers, and that, therefore, something else must have existed to do so. Its simplicity is unsurpassed. It will appeal even to those who ignore both the principles of mechanics and the action of Natural Selection. The figure 10 is placed on the surface of the right wing in Plate XV. In this region the dorsal surface of the wing is convex. A rule or "straight-edge" placed on the wing across this point, parallel to the ulna and resting upon the first and second digits, touches the wing along the whole of its length from number 10 backwards. In front of this the feather-surface curves downwards, so as to be perhaps 2 mm. below the edge of the rule near the digits. The *lower* surface of the metacarpal and of the first and second phalanges of the *second* digit lies fully 1 mm. above that feather-clad surface. The bones of the *third* digit are closely pressed down upon, but not sunk below, that surface. Therefore those digits did not lie *in* but *upon* the feathered wing when that animal finally sank dead upon the mud in which it has been preserved. Therefore, further, other bones (or bone) were present to support those feathers. No argument from embryology will shake that conclusion.

The *pelvis* is seen in the London specimen only, and in this specimen nothing is to be learnt from the left innominate, while even the right one is imperfect. This innominate appears to have been about 50 mm. long. The acetabulum is perforate. I believe there is no anti-trochanter, though in absence of the specimen I would not make the statement definite. It is characteristically avian pelvis so

far as concerns the length of the ilium and its prolongation to about an equal extent behind and in front of the acetabulum. If I mistake not, it is conspicuously unlike the pelvis of any existing bird in the matter of width, and the bearing of this will be shown in the sequel.

The *femur*, more slender than in existing birds of the same size, is strongly curved, the flexor surface being concave.

The *tibio-tarsus* is almost perfectly straight, and has only a small cnemial crest. The *fibula* is complete but slender.

The *foot* is a characteristically avian foot. In the Berlin specimen the matrix around the feet is so hard that a complete exposure of them has proved impracticable. The London specimen shows the left foot well. It is more massive and in every way larger than the corresponding parts of the Berlin specimen.

II.—The Feathers.

The evidence before us does not justify the expression of any opinion as to whether the body of *Archæopteryx* was covered with feathers all over or only partially. Three chief kinds of feathers are, however, recognisable in the fossils:—(1) quills, (2) coverts, and (3) contour feathers.

The *quills* are exceedingly well-preserved, especially in the Berlin specimen. The *remiges*, or wing-quills, had the characters of those of many ordinary birds, such as a pigeon. The calamus is not clearly seen, as it is hidden by the coverts; but the narrowing of the vane near the base shows (*e.g.*, in the second and third primary quills of the left wing of the Berlin specimen) that its length was much the same in proportion to the rest of the feather as in the corresponding feathers of a pigeon. The rachis is clearly seen, and is slightly curved so as to render the ventral surface of the wing concave and the dorsal surface convex. It tapers gradually as in feathers of the usual type. The groove seen along the dorsal surface of the rachis is probably due to shrinkage of the medullary substance during fossilisation—but this point is open to dispute. The vane, as in nearly all birds, is curved, the anterior and narrower moiety much more strongly than the posterior, which latter is overlapped dorsally by the anterior portion of the feather next following it. The barbs are easily seen, even in photographs; but I have been unable to make out the barbules

with certainty. Their existence, and even that of the hooks which serve to maintain the relative positions of the barbs, is safely to be inferred from the perfect regularity with which the barbs lie side by side in the Berlin specimen.

Of the quills, there are in each wing seven primary and ten secondary. The lengths of the primary quills, *i.e.*, of the quills borne by the metacarpals and phalanges, are as follows (commencing with the first) :—65, 90, 120, 125, 135, 130, and 120 mm. The secondary quills, borne by the ulna, are not easy to measure accurately, but they diminish gradually from the carpal region to the elbow. The first is 115 mm. long ; the last or tenth, 75 mm. Taken as a whole, these remiges, though less numerous than in most modern birds, are as perfectly fitted, by their form and arrangement, for the purpose of flight as in, say, a pigeon. Their size, though not difficult to determine absolutely, is difficult, if not impossible to determine relatively to the weight of the body ; for in our guesses at the weight of the animal a very large margin must be left for possible error.

The *rectrices*, or tail quills, differ very remarkably from those of any other known bird. Unfortunately, I overlooked the question as to their number when I was in Berlin. Previous authorities regard them as arranged in pairs, one pair to each vertebra of the tail, but Dames is very cautious on this point. My large photographs suggest that they are somewhat more numerous, but the point is one which may be left for the present undetermined. They differ from the corresponding feathers of modern birds of flight chiefly in size, being very much smaller than those of ordinary birds of equal size. Those of the anterior part of the tail are about 50 mm. long, or perhaps a little less (Berlin specimen). Further back they are longer, the maximum length of about 95 mm. being at about the twelfth caudal vertebra. To what extent, if any, they could be spread out and closed together we can only guess, and the fact that they lie in both specimens at an angle of about 30° to the axis of the tail does not help us much; for if the animal had the power of spreading its tail-feathers, this would perhaps have been effected by means of a muscle arising from some bone in the pelvic region, through the mediation of a slender tendinous band running along each side of the vertebral column of the tail, and opposed by a slender elastic ligament which would, when the muscle

was relaxed, bring the feathers into some such position as that which they occupy in the fossils known to us. These tendons and ligaments may well have been very small, and the absence of any trace of them in the fossils is not sufficient justification for our stating that they did not exist. We must, therefore, remain in ignorance as to whether *Archæopteryx* could or could not spread and close its tail.

Though the feathers are small, their great number gives to the tail, looked upon as an aëroplane, a very considerable surface, and this surface is greatly increased by the development of a series of feathers, which may for convenience be classed as rectrices, along the sides of the hinder part of the trunk. So far as I can make out by means of drawings that I have made to scale of the bird in the flying position, these lateral rows of feathers constitute with the tail-feathers a continuous aëroplane, extending forwards as far as the posterior edge of the extended wings. All those who have made drawings of the animal "restored," so far as I know, ignore the existence of this lateral aëroplane, and represent the lateral feathers of the tail-series as coming to an end in the tail, and the London specimen certainly suggests that this is the truth of the matter: the Berlin specimen, however, leaves no room for doubt as to the accuracy of the account I have now given.

Archæopteryx, unlike any other known bird, bore quills on its tibiæ. These are not either remiges or rectrices—and, indeed, the lateral aëroplane in front of the tail is not strictly made up of rectrices. In the absence of a better name, I will call them *tibial quills*. These *appear* to have lain in a single plane, which is the plane of flexion of the leg, the plane in which femur, tibia, and metatarsals all lie when the limb is bent; and they were apparently arranged in two series along the surfaces corresponding to the anterior and posterior surfaces of the human tibia, *i.e.*, the extensor and flexor surfaces. The number of them cannot be made out with certainty. The longest appear to have measured a little over 30 mm. in length. How they were placed in reference to the muscles I cannot say, and though they appear to have lain in a single plane, they may perhaps—though I do not believe it—have been "breeches," as they have been described. They extended along the whole length of the tibia, and certain appearances in the region between the left leg and the tail in the Berlin specimen suggest that the flexor-series extended also to the region of the femur.

Coverts are recognisable with certainty over the primary and secondary quills of the wings, especially the left wing, but they are not nearly so well preserved as the more robust quills. They appear to have been very slender, and now lie at an angle of about 40° to the quills. This deflection may have been due to the action of a stream of water passing over the dead bird when it first came to rest where it was finally fossilised; and, if so, the animal must have come to rest with its head up-stream, as one would naturally suppose.

The appearances in the fossil do not justify any statement as to the coverts in the tail or over the tibial quills.

Contour feathers may be recognised with certainty only in the cervical region. Three are well preserved between the right hand and the label bearing the number 11 in Plate XV. I believe I have recognised others ventral to the fourth and fifth cervical vertebræ; but this is far from certain. As to the covering of the rest of the body, we are in the dark.

III.—Habits.

Archæopteryx was an arboreal quadruped fitted for flight, if not for prolonged flight.

First, as to quadrupedalism and attitude.—I have already (p. 272) pointed out that the digits I, II, III of the hand are long and slender and flexible; and that each metacarpal and phalanx of these digits is curved, the concavity being ventral; and that the tubercles for the insertion of the flexor and extensor muscles of some of these phalanges are distinctly recognisable. To this I would now add that their joints are at different levels, showing that each finger could be flexed independently of the rest, and therefore that they were *free* and not bound together. I also showed that they did not support the quills, but were free from the wing except at their carpal ends. If they were bound together in the wing they would be inflexible, inasmuch as the joints of each digit are at different levels from those of the other digits.

The absence of that shifting backwards of the heavy abdominal viscera which is seen in such bipeds as birds, squirrels, kangaroos, dinosaurs, etc., and the lizard-like form of the body, are so clearly shown by the ventral ribs that it is obvious that its centre of gravity would be in front, not only of the acetabulum, but of the knee. If

the animal walked, or even stood, on two feet at all, it would have had to stand either bolt upright or with its dorsal surface directed slightly downwards. Whether the tail would then be on the ground (as in a kangaroo) or in the air (as in a squirrel) is open to doubt, for we do not know enough about the flexibility of its proximal portion to be able to say with certainty whether it could or could not be bent up over the animal's back. The presence of a long, heavy neck and massive head, which were supported by an elastic ligament, as shown by the curvature of the neck in the fossil (as in *Compsognathus* and the pterodactyles), add greatly to the force of this argument. A duck has to walk with its body tipped up almost on end, in spite of the great shifting of the heavy organs of the abdomen backwards between the legs. There is no room for doubt that in *Archæopteryx* the centre of gravity would be much further forward, not only on account of the heavy head and neck, but also on account of the solidity of the wing-bones, as shown by the absence of pneumatic foramina. Let any who doubt the justice of this argument compare the pelvis as seen in Plate XVI (which the authorities of the British Museum have kindly allowed to be prepared in illustration of this article) with the pelvis of, say, a pigeon or a dinosaur, or any other animal whatever capable of walking on two limbs in any but an erect position. The small size of the cnemial crests, moreover, forbids us to believe that the hind-limbs alone were able to bear the weight of the body when the knee was bent.

This bird was not only not a biped, but it did not walk on the ground at all. It would have been as helpless on the ground as a bat or even a sloth. The great length of the hind-limbs and shortness of the fore-limbs, at any rate when these latter were so flexed as to keep the feathers off the ground; the position of the shoulder joint, and especially of the articular surface of the humerus: these render the animal unfit for such a habit as even quadrupedal locomotion on the ground. The perfect state of the wing-quills at their tips shows that they were not brought habitually into contact with the ground, and I know of no rational argument in favour of the view that the animal did live largely upon the ground. For quadrupedal locomotion in trees the animal is admirably adapted. Long, flexible digits, provided with claws on all four limbs, fit it at least as perfectly to arboreal

quadrupedalism as *Galeopithecus* or *Petaurus* or any other "flying" mammal; and I think, from the greater length and flexibility of those digits, fit it even more perfectly for such a habit than even these mammals, and incomparably more so than the bats with their backwardly-directed hind limbs, which, while they serve to enable the animal to hold on to the tree or other body, are so modified for the support of the wing as to be of little use for quadrupedal locomotion.

As to flight.—*Archæopteryx*, though less well fitted for prolonged flight than most modern birds, was certainly capable of flight. As some have maintained that it was well fitted for powerful and prolonged flight, I will mention the features pointing to an opposite conclusion. The absence of a pectoral crest on the humerus, the small size of the sternum (*see* p. 269), and consequent relatively small size of the great pectoral muscle, indicate a deficiency of propulsive and sustaining power in flight. The absence of pneumatic foramina and consequent absence of air-cavities in the wing-bones show that rapid to and fro (*i.e.*, up and down) movement of the wing would involve a larger amount of exertion than in a wing with hollow bones as in most modern birds. It is not so much the extra weight that would be impedimental as the extra inertia. The narrowness of the body and smallness of the sternum indicate that the air-cavities of the abdomen, even if present, were smaller and less effective for respiration than in modern birds. I may be permitted here to make a remark as to the use of abdominal air-sacs in birds, or I may be suspected of having fallen into an old error of supposing that they materially diminish the weight of the bird. Flight involves, perhaps a greater, *i.e.*, more rapid, consumption of energy than any other form of locomotion, and all powerful fliers, whether birds or insects, are provided with respiratory organs of enormous effectiveness. In birds, instead of air being only pumped into the bronchial tubes and the rest being left to diffusion, the air is drawn tight through the lungs into the abdominal and other air-sacs, so that the highly vascular lung with its venous blood supply is brought into more direct relation with the "tidal air" than in mammals, while the "residual air," which is not changed at each double respiratory movement, rests, not as in mammals, in the lung itself, or at least not chiefly so, but in the air-sacs outside the lungs. The respiratory organ proper is thus brought into direct

relation with air capable of far more rapid renewal than in the mammalian lung. In other words, birds breathe the tidal air, while mammals breathe the residual air. *Archæopteryx*, however, shows no sign of the possession of large air-sacs, or of that large expanded sternum which, in modern birds of flight, insures the rapid change of the air by the same muscular movements as are involved in flight itself. While in all powerful fliers, both birds and insects, every movement of the wing insures a change of the air in the respiratory organ itself (and not merely in the passages leading to that organ), the form and structure of *Archæopteryx* forbid us to believe that such an adaptation existed in it.

Conclusions as to the size and efficiency of the heart might be drawn, but they are not only obvious but also perhaps a little risky; so I will leave them.

Nobody, except the constructors of flying-machines, seems to be ignorant of the fact that all powerful fliers have a wing-area which is very large in proportion to the area of the immoveable aëroplanes. Birds do not nowadays rely upon immoveable aëroplanes at all. The wings serve all the functions of both propulsion and sustentation, and the tail when used at all is used only for steering; while the vastly superior flight of insects is effected in the absence of any special steering apparatus, the wings themselves serving alike for propulsion, sustentation, and steering.

In *Archæopteryx*, then, we find an animal as yet not evolved beyond the aëroplane phase of flight; a phase characterised by the use of large aëroplanes, which, while offering considerable resistance to flight, take no part in the propulsion. It may further be pointed out that among flying things, whether birds, mammals, insects, or flying machines, the most efficient are all far broader from side to side than they are long. Lilienthal, alone among men who seek to fly, seems to have appreciated the real bearing of this fact. The further mechanical consideration of the point, even as applied to *Archæopteryx*, would, however, take us too far. It is sufficient for my present purpose to have pointed out wide differences of structure both as to the immediate organs of flight and also as to the propelling muscles and the respiratory organs on which powerful flight depends, between, on the one hand, *Archæopteryx*, and, on the other hand, all other flying

animals. I will only add an argument for the benefit of biologists who may be unable to grasp the significance of mechanical considerations. The oldest known bird—*Archæopteryx*—was constructed, so far as the sustentatory apparatus of flight was concerned, on a principle which has been superseded in all modern birds, and which may therefore be safely pronounced, even on purely biological grounds, to be inferior in effectiveness to the principle of construction which has superseded it.

Archæopteryx was, therefore, not a very good flier. How good it was as a flier, I dare not guess; though the perfect, but rather small, wings strongly suggest that, in spite of the impediments I have mentioned (free digits, heavy head and neck, large aëroplanes offering resistance to rapid movement, small muscles, heavy non-pneumatic bones, and deficient respiratory apparatus), *Archæopteryx* could fly better than the competing pterodactyles.

Since the days of *Archæopteryx*, its descendants, or the descendants of its near relatives, have been evolved into the modern bird, which, in its more perfect forms, is a perfect biped and a powerful flier: and a brief enumeration of some of the chief changes involved in that evolution will throw an additional light upon my contention as to the comparatively small power of flight, and as to the quadrupedal locomotion of *Archæopteryx*. The shoulder has shifted backwards, the trunk has become shorter, bringing both elbow and knee-joints nearer the centre of gravity; thereby rendering balance in walking or standing independent of the aid of the fore-limb. The fore-limb, in accordance with this release from one of its functions, has lost the digits I, II, and III on which that function depended, and has thus been reduced in inertia, while the pelvis has become widened to allow for the backward displacement of the abdominal viscera, and the tibia has acquired a cnemial crest of much greater size, enabling the hind-limb to support the weight of the whole body, with the knee flexed and placed in such position that the centre of gravity is behind it. The aëroplanes of the tibiæ have been abolished, and that of the tail shortened, lightened, and reduced to a steering apparatus pure and simple. The wings have gained in size; their inertia has been reduced by the development of air-cavities in the wing-bones; more powerful muscles have been evolved for the movement of the wings, and this has involved the

development of a pectoral crest and of a large sternum. The reduction in weight of the head (especially jaws) has aided in the backward shifting of the centre of gravity. The development of the large sternum has facilitated the evolution of a respiratory apparatus of more efficient type, and the shortening of the whole body and concentration of its weight near one point, aided by the stiffening of the back—often by ankylosis of the vertebræ and always by the increase in length of the functional "sacrum" has rendered the support of the hinder part of the body by cumbrous aëroplanes unnecessary.

IV.—Answers to Critics.

Many and various arguments have been urged against my view as to the homology of the digits of the wing of an ordinary bird, as well as against my interpretation of the *photograph of Archæopteryx* and other contentions contained in an article on sources of error, which was published in "Natural Science" (Vol. III. p. 275).

Mr. Pycraft asks (p. 445), Where did my supposed but unseen digits IV and V articulate in *Archæopteryx?* I have answered this already in the preceding pages of this article; but there is good reason for answering it again. The digits did exist, and their metacarpals are conspicuous in the London specimen, and they articulated to that large rounded carpal bone which is shown at the distal end of the radius and ulna of the right wing in Fig. 2, p. 116.

Mr. Virgil L. Leighton, in No. iii. of "Tuft's College Studies," says (p. 71), "That there is developed a fourth digit in the avian manus is beyond question [!], and the fact that this comes upon the ulnar side of the three permanent fingers is sufficient to invalidate the nomenclature III, IV, and V of Hurst." The "plausibility" of my view is, moreover, founded on ignorance, and "no one without a theory to support would regard it [*i.e.*, what I called *os pisiforme* in Nat. Sci., Vol. III., p. 279] other than a digit." Mr. Leighton, of course, knows that greater men than myself regard the *os pisiforme* itself as the remnant of a digit; but even if he did not, the alleged resemblance of it to a digit in a certain stage in the development of a certain bird (*Sterna*) would not in the least affect my conclusions. It is not difficult to name a few mammals in which things occur much more like digits beyond the normal five than the embryonic rudiment he refers

to. (N.B.—Rudiment = beginning, germ, thing as yet undeveloped, "Anlage.")

Only one really strong and rational objection to my views has come to my notice. It was urged in conversation by Dr. Jaekel, of Berlin, and subsequently by Professor Dames. They urge the principle, well-known among palæontologists, that in all fossils we must expect the evidence of things below the surface to appear on the surface; that all the bones of a single specimen usually lie nearly in a single plane. The bones of *Archæopteryx* in the Berlin specimen certainly do all lie almost in a single plane. There is, however, no evidence in that specimen of the existence of the supposed digits IV and V. What I formerly took for a shadow in the photograph (*see* 12, Plate XV.) is merely a yellow stain on the slab (but not without significance), and the slender digits I, II, and III are not crushed or distorted as if by underlying bones; the tibial quills, as I have called them, of the right leg do unmistakably show a displacement or distortion where they lie over the left knee; vertrebral and ventral ribs lie in juxtaposition, and so even do the ribs of right and left sides.

This, however, not only ceases to be an objection, but actually comes to support my view when we enquire more closely into it. Many fossils are distorted much as they would be by enormous vertical pressure: they are flattened much as wax models of them would be by being put in a hydraulic press and squeezed. But *Archæopteryx* is not so distorted The skull is not flattened: its cavity was empty, and not either filled with matrix or abolished by the collapse of its walls. The left femur does *not* lie in the same plane as the right, but so inclined that its head is now deeply embedded in the slab, while that of the right lies well above the general surface of the slab. The digits do not lie all in one plane; in the right hand the second lies over the third crossing it without displacement and without deformation. On the other hand, the first metacarpal lies *lower* than the second, and not above it as it should in the natural position of the parts. The second metacarpal and proximal phalanges lie, not in the same plane as the feathers, but well above that plane. Whatever flattening there might have been it could not have *lifted* the second digit well above the level of the *proximal ends* of the quills it was supposed to have supported. The bones of a dead bird, which has fallen on the bottom of a stream, or

lake, or sea, will naturally fall to the level of the underlying deposit as fast as the decay of the soft parts allows them to do so. The weight of overlying deposits may even flatten out ribs and bring them all to one level. It may even crush the bones where they lie one over the other—I am not sure that this has not occurred in the left hand—but it has not, in this case, crushed the skull, or the phalanges of the third digit of the right hand, or the pelvis; and it has not brought the proximal ends of the two femoral bones into juxtaposition. Had it brought the digits IV and V to the same level as I, II, and III, we should have seen them, and these latter might well have been crushed by them; but the perfect preservation of these digits, even where they cross each other, and the fact that they do lie, especially the second, well above the level of the feather-surface, shows that there has been n this case little, if any, deformation by pressure of overlying strata; hence the absence of all trace of digits IV and V on the surface. If any such deformation had occurred it would have brought II and III to the level of the feather-surface. No matter, therefore, what pressure there may have been, the fact that those digits II and III lie now above that surface shows that they did originally lie above it, and not below it as all views except my own demand.

C. HERBERT HURST.

LITERATURE REFERRED TO IN THE FOREGOING ARTICLE.

OWEN.—*Phil. Trans.*, 1863.

DAMES.—Ueber Archaeopteryx. Berlin, 1884

PYCRAFT.—*Natural Science.* Vol. 5, p. 350 and p. 437.

LEIGHTON.—*Tufts ollege Studies*, No. III.

HURST.—*Natural Science.* Vol. 3, p. 275 ("Errors")

" " " Vol. 6, p. 112, p. 180, and p. 244.

(The present article is in large part reprinted from NATURAL SCIENCE, *Vol. 6.)*

EXPLANATION OF PLATES.

PLATE XIV.

Photograph of left wing of *Archæopteryx*, from the specimen in the Natural History Museum, Berlin (*two-thirds nat. size*).

PLATE XIV.

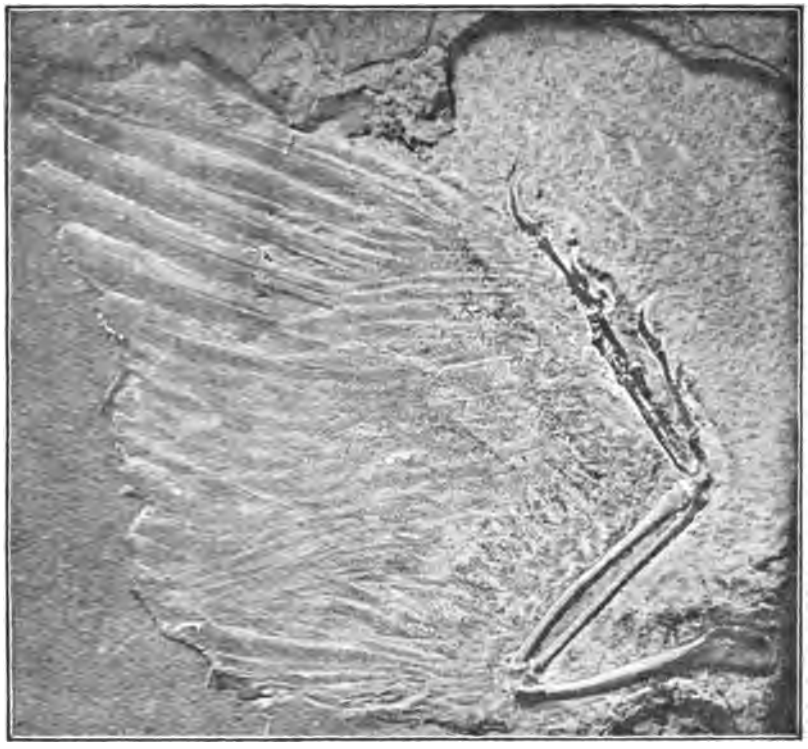
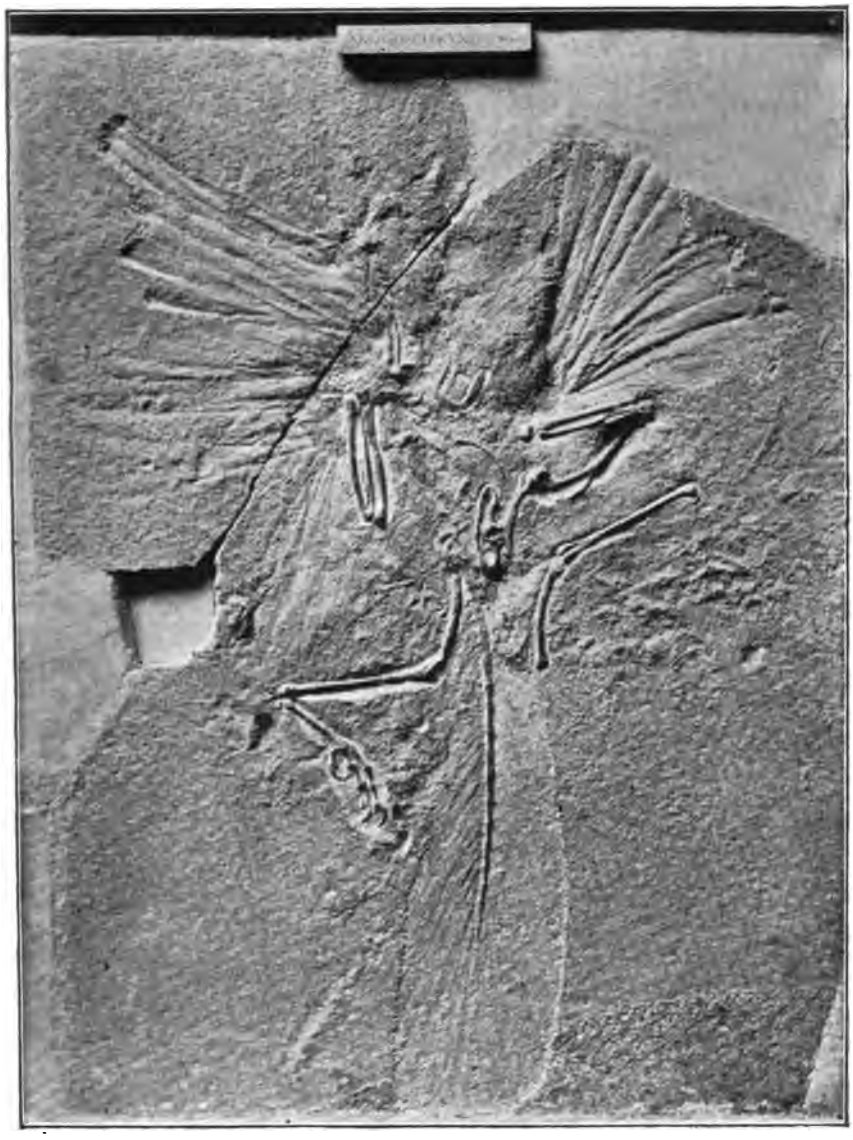


PLATE XV.

Reprinted from NATURAL SCIENCE, vol. vi.

PLATE XVI.



Reprinted from NATURAL SCIENCE, vol. vi.

PLATE XV.

A photograph of the Berlin specimen of *Archæopteryx* taken before the skull and certain other parts were as fully exposed as they now are. (Scale 5 : 17).

1. First digit of left manus. 2. Second ditto. 3. Third ditto. 4. Radiale of left carpus. 5, 6, 7. First, second, and third digits of right manus. 8. Region of right wing which in the specimen lies lower than the visible bones of the hand and lower than the region marked 10. 9. Primary quills of right wing. 11. Small portion of matrix lying upon proximal end of humerus. (See reference to this in the text.) 12. Yellow stain resembling, in the photograph, a shadow. 13. Cnemial crest. 14. "Abdominal" or ventral ribs. 15. Feathers of crural aëroplane. 16. Joint between second and first phalanges of third digit. 17. Left femur.

The specimen was illuminated at the time of photographing by light falling upon it from above and in front and slightly to the left.

PLATE XVI.

ARCHÆOPTERYX.

From a photograph, one-quarter natural size, of the specimen in the British Museum (Natural History), taken by kind permission of Dr. Henry Woodward, F.R.S., Keeper of the Geological Department.

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